ANATOMY OF CERTAIN GOLDENRODS[1]

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(WITH PLATES VII AND VIII AND ONE FIGURE)

In dealing with the anatomical features of *Solidago*, and especially in studying the modifications of its woody cylinder in relation to the leaf trace, it is well to bear in mind the fact that the goldenrods belong to a family which occupies a high place systematically. The largest proportion of herbs and short-lived perennials, especially in temperate regions, belongs to the Compositae; and since they are so generally admitted to be high forms, a certain amount of evolutionary progress can be taken for granted in studying them. Another advantage in investigating genera of the Compositae is the fact that in the family and in any genus of the family both the woody and herbaceous type of stem may be found; hence comparisons are more easily made and conclusions more readily drawn. Not only within the same genus are both kinds of stem to be found, but the same aerial axis has regions which are characteristically woody and herbaceous. This situation is well illustrated by *Solidago*. In the lower portions of the aerial axis, as well as in the subterranean parts of the stem, the organization is typically woody; while in the higher and more slender portions of the stem the herbaceous type prevails. In short, *Solidago* presents an epitome of a woody-herbaceous condition in which the transition from one type to the other is advantageously elucidated.

The species of goldenrod studied were *Solidago canadensis*, *S. bicolor*, *S. rigida*, *S. caesia*, *S. speciosa*, *S. sempervirens*, *S. graminifolia*, *S. latifolia*, *S. serotina*, and *S. patula*. It was found that in all these species there are certain modifications of the woody cylinder related definitely to the leaf strands. These consist in the transformation of portions of the woody segment through which the leaf trace takes its departure into parenchyma and in the elimination of fibers and vessels.

[1] Contributions from the Laboratories of Plant Morphology of Harvard University.

There are, as a rule, three traces to each leaf in *Solidago*, a median and two laterals. In some species (for example, *S. rigida*, *S. patula*, and *S. sempervirens*) there is a multiplication of traces, correlated apparently with the increased size and vigor of the plants and especially with the size of their leaves. The species mentioned, besides being very large and leafy, are characterized by having large, full heads of flowers.

In studying the modifications of the woody cylinder, the median trace need not be especially considered, since conditions here are complicated by the presence of the axillary bud. Attention accordingly may be directed to the lateral traces, which present a simpler situation. The most conservative part of the stem is at the node; and conditions at the node, therefore, are the most significant. A section cut transversely through the node of the woody axis of any of the species of *Solidago* mentioned shows the leaf traces still in the cortex. Following the traces down in serial sections, it is to be noted that they enter the woody cylinder a short distance below the node and are surrounded on all sides by parenchyma. One leaf trace usually passes into the stele at a higher level than the others. Consequently, sections cut at different distances below the node show the traces in different topographical relations. For a considerable interval downward the trace is surrounded on all sides by parenchyma, so that the storage elements are present not only on the sides of the trace but confront it externally as well.

Fig. 1 shows a transverse section of *S. canadensis* cut far enough below the node so that only one of the lateral traces (the one on the right which entered the cylinder much lower than the corresponding trace on the left) appears surrounded on all sides by parenchyma. Figs. 2, 3, and 4 show this situation under higher degrees of magnification and in the three dimensions respectively. Fig. 2 is a high power representation of the transverse section of a lateral leaf trace segment of *S. canadensis*. The foliar strand can be seen lying at the bottom of the figure, obviously surrounded by storage parenchyma, which both confronts it radially and lies on either side of it. In this section it is clear that a portion of the cylinder opposite the leaf trace has undergone considerable modification, apparently in relation to the photosynthetic activity of the leaf. The cauline segment in relation to it may conveniently be designated as the leaf trace segment. Fig. 3 shows the same situation in longitudinal tangential aspect. Here the trace appears high up in the center of the figure and is obviously surrounded on all sides by parenchymatous tissue. This section was made near the region of the cortex, so that it represents the leaf strand after it has become horizontally inclined. Fig. 4 is a radial view of the same situation, illustrating in a similar manner the imbedding of the leaf trace in storage tissue in its course through the woody cylinder. This section also demonstrates the fact that vessels and fibers again make their appearance in the cylinder directly above the leaf trace segment after the foliar strand has passed into the cortex.

It is clear from the foregoing illustrations that the woody cylinder opposite the leaf trace undergoes certain modifications in relation to the activity of the foliar organ. The strand as it passes upward and outward through the cylinder is flanked on either hand by storage tissue which may be designated as flanking parenchyma. Farther in its outward course, and more marked where the cylinder is thick, subtending the trace externally is a mass of tissue which may appropriately be called subtending or confronting parenchyma. Above the trace is the parenchymatous interval known as the leaf gap. It is noteworthy in this connection that the leaf trace in the thick or woody cylinder (and all the axes here figured are aerial) of *S. canadensis* has the same topographical relation to storage devices as is found in arboreal types like *Quercus, Casuarina,* etc. The origin and topographical relations of the broad ray in the oak have clearly and convincingly been elucidated by EAMES,[2] and the conclusions reached by this author have been shown by BAILEY[3] to hold with equal validity for the Betulaceae and Fagaceae in general. EAMES[4] has also shown that the woody type in the Rosaceae is subject to the same general modifications in relation to the leaf trace as obtained in the Betulaceae, Fagaceae, and also,

[2] EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**:161–167. 1910.

[3] BAILEY, I. W., Relation of leaf-trace to compound rays in lower dicotyledons. Ann. Botany **25**:225–241. *pls. 15–17. fig. 1.* 1911.

[4] EAMES, A. J., Herbaceous type in angiosperms. Ann. Botany **25**:215–224. *pl. 14.* 1911.

as has been shown, in the woody aerial stem of *Solidago*. It is clear that there is a general agreement regarding the part the leaf trace plays in relation to the transformation of portions of the woody cylinder into a parenchymatous segment.

Concerning the comparableness of woody types like the oak, etc., with those presented by axes characteristically herbaceous, however, some doubts have been raised. It has, for instance, been maintained by SINNOTT and BAILEY[5] that the herbaceous type does not come from the woody through the conversion of secondary xylem opposite the leaf strand into storage parenchyma, but, on the contrary, that the evolution of herbaceous forms has come about through the reduction in amount of secondary wood and increase in width of the broad rays. This, together with their decrease in radial extent, has resulted in the confining of the storage tissue in herbaceous axes to the sides of the leaf trace, with the result that parenchyma in no case subtends the trace as in the oak, etc. "In practically all families of herbs, the interfascicular parenchyma is never subtended by a tiny leaf trace bundle of protoxylem, but always abuts directly on the pith tissue between the strands of primary wood" (*loc. cit.* p. 596). Hence it is assumed that the significant conditions in the woody stem in relation to the leaf trace are in no way responsible for the origin of the herbaceous form. It is further claimed, in substantiation of this hypothesis, that the condition outlined for the Betulaceae, etc., while it holds for the subterranean parts of the woody axis, does not explain the situation in the aerial region of the herbaceous stem where "the actual evolutionary development must have taken place (*loc. cit.* p. 555).

The situation in the herbaceous part of *Solidago* may be described. Fig. 5 represents a slender stem of *S. canadensis*, which is obviously herbaceous. The section was made just below the node and shows the three leaf traces at the top. At the bottom and a little to the right, the three traces of the next higher node may be seen. In the upper part of the figure, even under the comparatively low power of magnification, it can easily be noted that the

[5] SINNOTT, E. W., and BAILEY, I. W., Investigations on the phylogeny of the angiosperms. IV. The origin and dispersal of herbaceous angiosperms. Ann. Botany **28**:547–600. *pls. 39, 40.* 1914.

traces pass out surrounded by parenchyma. Fig. 6 is a more highly magnified view of one of the lateral leaf traces, showing that even in the upper aerial region of this persistently woody species confronting as well as flanking parenchyma is present. Fig. 6 also elucidates the relatively greater size of the leaf trace in proportion to the segment, as compared with fig. 2. Allowing for the difference in the size of the leaf trace and for the inevitable thinning of the cylinder in the more slender portions of this particular stem, as well as in herbaceous forms generally, one can readily see how, if the cylinder were sufficiently reduced in size, the subtending storage tissue would be confined to the sides of the foliar strand even in the region of the node. Lower in the internode there would normally be only flanking parenchyma, since the central region of the confronting parenchyma is transformed below into a characteristically woody segment composed of vessels, fibers, etc. EAMES (*loc. cit.*) has made it clear that in the Rosaceae in which both woody and herbaceous types occur the latter has undoubtedly come from the former by the parenchymatous transformation of more and more secondary wood in proximity to the leaf traces. Hence the bundles of the herbaceous stem represent ordinary woody segments interspersed with other segments which have undergone the parenchymatous metamorphosis described.

It would seem fairly clear from the preceding descriptions that the highest dicotyledons present the same general conditions of modification of the originally woody cylinder in relation to storage and the leaf trace as is found in the lower groups, such as the Betulaceae, Fagaceae, etc. It is quite clear that the herbaceous type has originated in a similar manner and largely as the result of the thinning of the woody cylinder. *Solidago* obviously illustrates this transition stage, since it shows in its herbaceous regions the same topographical relation to the cylinder as is found in the typically woody part of the axis. To elucidate this point, and chiefly for the sake of making the situation indubitably clear, the accompanying diagrams have been introduced.

In text fig. 1, *A* represents the woody portion of *Solidago*, and would also hold equally well for the woody dicotyledons with large foliar rays. On the other hand, *B* elucidates the characteristic herbaceous condition in a dicotyledonous stem. In *A* the condition presented by figs. 2, 3, 4, and 6 is illustrated. The departing leaf traces in the region of the node, especially as they bend outward through the cylinder, are both flanked and subtended by storage parenchyma, a situation shown diagrammatically in black. *B* illustrates the topography of the herbaceous region of the stem in the Compositae, where, by reason of the greater relative importance of the leaf trace, its radial diameter nearly equals that of the ordinary xylem segments of the cylinder. As a consequence, the confronting parenchyma of *A* is conspicuously absent and the storage

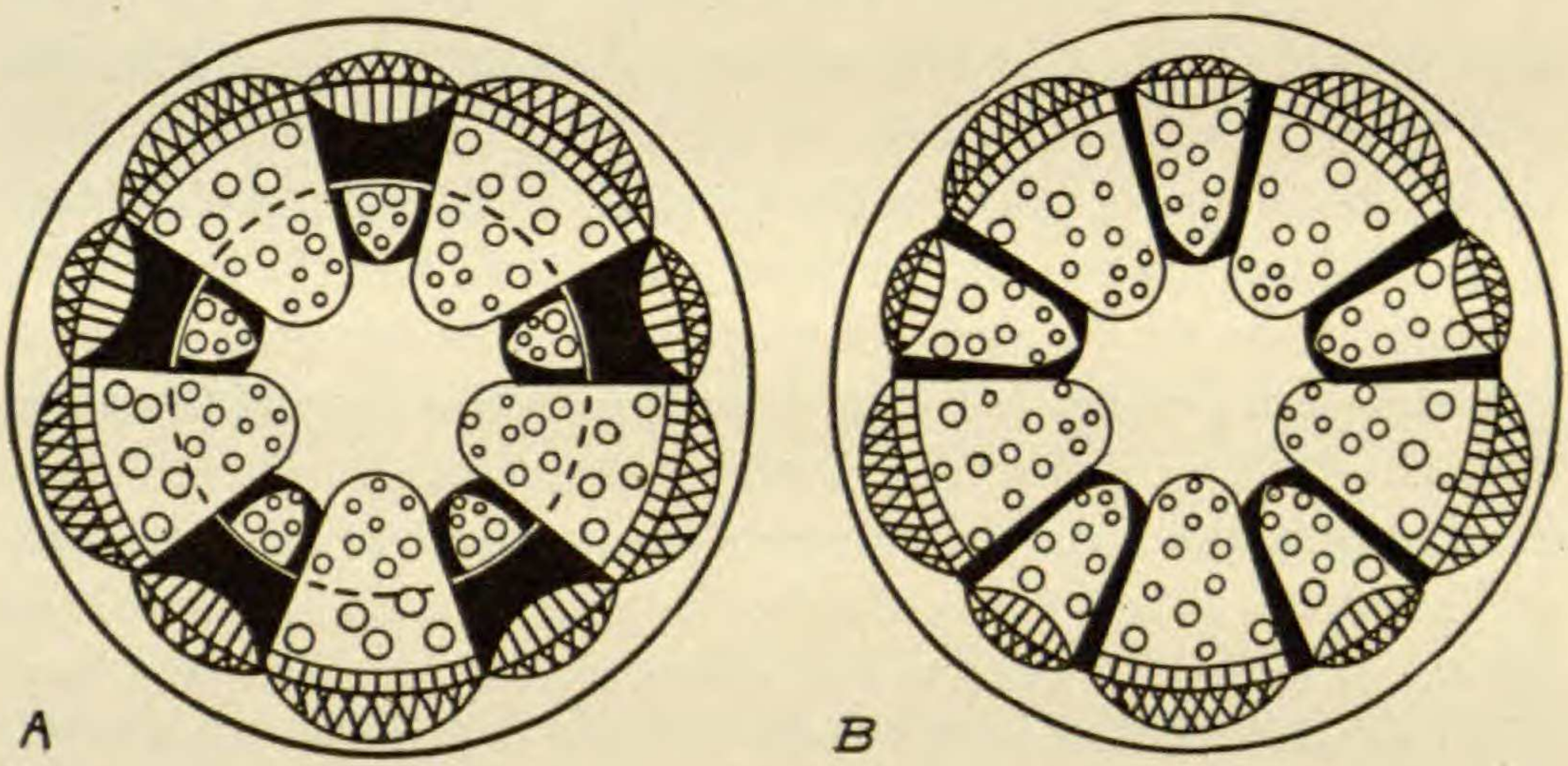

FIG. 1

tissue, as a necessary geometrical result, is confined to the flanks of the narrower segments representing the foliar strands. This exaggeration of the leaf trace in the herbaceous type is probably in response to the greater relative size and importance of the leaves. That the situation outlined in *B* obviously results from the thinning of the cylinder, with the consequent confining of the storage tissue exclusively to the sides of the trace, will be evident by referring to *A* and supposing the woody cylinder here to be considerably reduced in thickness. This hypothetical thinning of the cylinder is represented by a broken line drawn through the stele just outside the leaf traces. A comparison of the portion of the cylinder thus limited in *A* with the herbaceous type represented in *B* shows that the conditions inside the broken line are substantially the same as those depicted in the latter illustration. The parenchyma in both is flanking only and the leaf trace plays a predominant part.

Hence, from a consideration of the situation obtaining from the lower dicotyledons to the Compositae, it would seem clear that the herbaceous type has been derived from the woody through the conversion of segments related to the outgoing leaf strand into wood parenchyma; and that in extreme herbaceous types the storage tissue has become confined to the sides of the trace by the simple process of the thinning of the cylinder and the increased relative importance of the foliar strand.

An interesting feature of some species of *Solidago* is the multiplication of leaf traces, a situation which might be expected in relation to the increased efficiency of the leaves. As has been stated, the usual number of traces in this genus is 3; but in more vigorous stems the leaf traces may be more numerous. In *S. patula*, for instance, there are 5; and in *S. sempervirens*, the salt marsh goldenrod, there are as many as 7 or 9, according to the vigor of the plant. This condition is represented in fig. 7, which is a transverse section of *S. sempervirens*. In the instances where there is a multiplication of leaf traces, it is noteworthy that in addition to stout and leafy stems, these species are likewise characterized by unusually large and full heads of flowers.

Another point of interest, which is of course a common anatomical characteristic of the Tubuliflorae, is the presence of oil canals in the pith or cortex, or in both. In fig. 7, which is a cross-section of *S. sempervirens*, these oil canals may easily be noted in both pith and cortex; and in fig. 5, which represents the same plane in *S. canadensis*, they are visible in the cortex only.

An additional feature of interest is presented by the leaf bundles in the cortex, namely, the presence of internal phloem. This is shown in fig. 8, which is a high magnification of one of the cortical bundles of *S. sempervirens*. Other species of *Solidago*, for example, *S. canadensis*, *S. patula*, *S. rigida*, etc., show the same organization of their cortical bundles, and it seems to be a general condition for the genus. It has been suggested by WORSDELL[6] in the case of the Cucurbitaceae that internal phloem is a "vestigial structure." In

[6] WORSDELL, W. C., The origin of medullary (interxylary) phloem in the stems of dicotyledons. Ann. Botany **29**:567–590. *figs. 10*. 1915.

this family (the Cucurbitaceae), as is well known, the stem bundles are characterized by the presence of internal phloem. The conclusion has been reached by this author, as a result of the study of the conservative regions, that the internal phloem is derived from inversely oriented medullary bundles fused with the inner surface of the woody cylinder. The situation in *Solidago* (and in other genera of the Compositae) is of interest in this connection, especially as the presence of internal phloem is so constant a feature of the organization of the leaf trace in its course through the cortex. Since the results of comparative anatomical study of existing and extinct gymnosperms show clearly the conservative character of the leaf trace, it seems fairly obvious that the Compositae once possessed internal phloem in the stem like the Cucurbitaceae, Solanaceae, etc., but have lost it as a result of subsequent modifications. It may be pointed out that this assumption accords with the high systematic position ordinarily assigned to the family. This conclusion is in no way weakened by the fact that the Compositae are actually included in the same large group or cohort as the Cucurbitaceae, namely, the Campanulales (Campanulatae).

In *Solidago* and most genera of the Compositae there are depressions in the woody cylinder corresponding to the leaf trace segments. Work carried on in this laboratory by Mr. J. P. Poole on *Helianthus* has demonstrated that in this genus the depressions invariably correspond to the foliar segment. Fig. 9, which is a woody stem of *H. hirsutus*, is inserted here because it illustrates this situation so diagrammatically. At either side two median traces are to be seen, and also their two corresponding lateral traces, making in all 6 depressions in the cylinder and 6 corresponding parenchymatous modifications. Most species of *Solidago* show similar depressions in immediate relation to the foliar segment. Bailey[7] has made it clear that in the oak these depressed segments are caused by the retarding influence on growth of pairs of closely approximated compound foliar rays. The depressions in the Compositae in relation to the leaf trace segments are likewise connected with growth mechanics.

[7] Bailey, I. W., The evolutionary history of the foliar ray. Ann. Botany **26**:647–661. *pls. 62–63*. 1911.

The situation in the oak, however, is somewhat different from that outlined for *Helianthus* and the Compositae generally; for in the oak the depressions are xylem segments *between* the lateral compound leaf rays and do not correspond to the leaf trace segment itself as in the Compositae. For purposes of elucidation the situation presented by the oaks may be briefly reviewed. In *Quercus* the two predominant lateral traces of each foliar organ are related to foliar rays which are typically in 5 pairs, corresponding to the two-fifths phyllotaxy of the oak. Between these approximated pairs of rays there is a "dipping in" of the cylinder as a consequence of the retarding influence on growth of the rays in question.

In some genera of the Compositae we get a situation approximating that in the oaks, and as a result contrasting with that figured for the sunflower, etc., in fig. 9. In *S. graminifolia*, for instance, the depressions do not correspond to single leaf trace segments as is usual in the Compositae, but are in relation to the xylem segments between the leaf rays. This situation may be noted in fig. 10, a section of *S. graminifolia* cut in the region of the node. The result of the depression of segments between the rays is that the stem is roughly divided into 5 parts as in the oak. The pith is 5-angled and the median trace comes off opposite an angle of the pith precisely as in *Quercus*. Fig. 11 shows a portion of the same more highly magnified, illustrating how striking is the depression and how clear the analogy to the oak. Fig. 12, which at first sight might easily be taken for a section of an oak twig, is really a transverse section of *Aster multiflorus*, and elucidates this phenomenon even more strikingly. Here there can be no doubt that the depressions in the cylinder occur between pairs of rays exactly as in *Quercus*, and do not correspond to single leaf trace segments. This topographical condition of the stem is rare in the Compositae, although it is occasionally present in *Solidago*, as for example in *S. graminifolia*, and is extremely common in the genus *Aster*.

Summary and conclusion

Solidago is a genus which occupies a very high place systematically and presents both woody and herbaceous types of stem, not only in the genus but also in different regions of the axis of the same species. The modifications of the stem, especially the transition from one type to the other, therefore, can be studied to good advantage in this and other genera of the Compositae.

In connection with the derivation of the herbaceous type it has been shown that the general principles derived from the study of the Betulaceae, Fagaceae, Rosaceae, etc., hold equally well for this particular genus of the Compositae. Here as there the same storage modifications result from the transformation of woody tissues surrounding the outgoing leaf traces. No vessels appear in the leaf trace segment in the region just below the node, but at a lower level in the internode the foliar segment again becomes woody with typical vessels and fibers.

In the slender herbaceous part of the aerial axis the same general situation obtains. The traces, however, are relatively well developed in proportion to the size of the segment, and the cylinder as a whole is thinner. This thinning of the cylinder automatically results in the limiting of the storage elements to the flanks of the foliar strands in extreme herbs.

It seems noteworthy that in some species of *Solidago*, for example, in *S. sempervirens*, but occurring also in other species, there is a multiplication of the foliar traces which seems to be definitely correlated on the one hand with greater vegetative vigor and on the other hand with more numerous and larger heads of flowers.

Internal phloem in the leaf bundles of the cortex is a general feature of the genus and probably of the family. It seemingly perpetuates a condition which was once characteristic of the bundles of the axis.

Solidago occasionally resembles the oak anatomically by the "dipping in" of woody segments between the leaf rays in contrast to depressions in the cylinder corresponding to single leaf trace segments, as in *Helianthus* and the Compositae generally. The depression of the cylinder between leaf rays is the usual situation in the genus *Aster*, which, with certain species of *Solidago*, are exceptions to the general rule for the Compositae.

In conclusion I wish to thank Dr. E. C. JEFFREY, under whose direction this investigation has been carried on, for material, valuable advice, and suggestions.

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EXPLANATION OF PLATES VII AND VIII

FIG. 1.—Transverse section of woody stem of *Solidago canadensis;* ×10.

FIG. 2.—Lateral leaf trace segment of same more highly magnified; ×50.

FIG. 3.—Tangential view of same; ×60.

FIG. 4.—Radial view of same; ×60.

FIG. 5.—Transverse section of upper and more herbaceous region of *S. canadensis;* ×15.

FIG. 6.—Lateral leaf trace segment of same more highly magnified; ×120.

FIG. 7.—Transverse view of section of *S. sempervirens* showing multiplication of leaf traces; ×12.

FIG. 8.—Leaf trace bundle of same section more highly magnified; ×150.

FIG. 9.—Transverse section of woody stem of *Helianthus hirsutus;* ×10.

FIG. 10.—Transverse section of *S. graminifolia;* ×8.

FIG. 11.—Part of thinner cylinder of same species more highly magnified; ×40.

FIG. 12.—Transverse view of section of *Aster multiflorus;* ×12.